SPATIAL AND HABITAT RELATIONSHIPS OF RED-EYED AND BLUE-HEADED VIREOS IN THE SOUTHERN APPALACHIANS

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ABSTRACT.—Red-eyed (*Vireo olivaceus*) and Blue-headed (*V. solitarius*) vireos have similar foraging ecologies, similar songs, and occupy similar forest habitats. Evidence suggests, however, that the typical pattern of habitat and foraging segregation in sympatric vireos may not be observed in the southern part of their range of sympatry. We tested the degree of ecological overlap in the southern Appalachians of Virginia by asking whether these species segregate via interspecific territoriality or habitat use. We quantified response to heterospecific song, territory overlap, and habitat characteristics during the breeding seasons of 1997 and 1998. Red-eyed and Blue-headed vireos responded at low frequencies (9% and 2%, respectively; years combined) to the songs of the other species. Not surprisingly, given the playback results, approximately 54% of territories examined for each species overlapped with a territory of the other species. Within territories, both vireos used structurally similar habitat. Microhabitat composition, however, differed between species. Blue-headed Vireos occurred in areas with greater abundance of white oaks (*Quercus* spp.), conifers, and snags, whereas Red-eyed Vireo habitat had qualitatively greater abundance of red oaks and red maples (*Acer rubrum*). Red-eyed and Blue-headed vireo habitat was discriminated further by the presence of striped maple (*A. pensylvanicum*) and black locust (*Robinia pseudoacacia*) in the canopy of Red-eyed Vireo habitat, whereas conifers and black birch (*Betula lenta*) were more common at sites where Blue-headed Vireos were observed. Shrub species composition did not differ significantly between vireo habitats. Red-eyed and Blue-headed vireos showed only subtle habitat segregation at our study site in the southern Appalachians, and we found little evidence of interspecific aggression. *Received 6 June 2001, accepted 3 February 2002.*

The study of avian niche relationships provides information about patterns of segregation among coexisting species that is prerequisite to identifying the ecological mechanisms structuring avian communities. Birds of the genus *Vireo* provide a good system for studying niche overlap because species pairs interact in different combinations in different settings. Vireos show considerable dietary overlap (Chapin 1925) and they are broadly sympatric (Price et al. 1995), but they rarely coexist within a habitat (Hamilton 1958, 1962; Cody 1985). When vireos do share habitat, they typically show either horizontal or vertical segregation into different microhabitats (Hamilton 1958, 1962) and often differ in body size (Cody 1985). Such consistent patterns of segregation in various species pairs has been interpreted as evidence for the importance of competition in vireos (Hamilton 1962, Cody 1985). However, some assemblages of vireos do not conform to these patterns, and their ecological relationships may be particularly instructive.

For example, Red-eyed (*Vireo olivaceus*) and Blue-headed (*V. s. solitarius*) vireos are similar in size (15.0–17.0 g) and widely sympatric in the forests of Canada and the eastern United States during the breeding season (Price et al. 1995). Over most of this area of sympatry, the two species have similar foraging ecology (Chapin 1925, Williamson 1971, Holmes et al. 1979, Robinson and Holmes 1982) but occupy distinct habitats. Red-eyed Vireos typically inhabit well-developed, deciduous forests (Bent 1950, Hamilton 1962, James 1971) with some shrub understory (James 1971), whereas Blue-headed Vireos inhabit middle-aged to mature evergreen forests with sparse understory (James 1998) or mixed deciduous-coniferous forests (Bent 1950, Hamilton 1962). This pattern, exhibited in the northern part of the range of sympatry, is typical of vireos, but it appears to break down between these species in areas of sympatry in the southern Appalachians where Red-eyed Vireos coexist with a subspecies of Blue-headed Vireo (*V. s. alticola*, hereafter Blue-headed Vireo). Our observations suggest that there is considerable overlap in habitat use between Red-eyed and Blue-headed vireos

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in the southern Appalachians, and available information (Rabenold 1978, Petit et al. 1990) suggests that these two species may be more similar in foraging ecology in this region as well. However, no studies have quantified the interactions between these species in the southern Appalachians.

The objective of this research was to quantify ecological factors potentially influencing coexistence between these two species in the southern Appalachians at the level of horizontal habitat segregation. In this study we considered the potential for interspecific aggression by determining if Red-eyed and Blue-headed vireos responded to playback of songs of the other species or held mutually exclusive territories. We also quantified habitat characteristics to determine if Red-eyed and Blue-headed vireos used different microhabitats within the available habitat.

STUDY AREAS AND METHODS

Study areas.—We conducted this research from 12 June to 16 July 1997 and 17 April to 15 June 1998 at the Univ. of Virginia's Mountain Lake Biological Station (MLBS) and adjacent Jefferson National Forest in Giles County, Virginia (37° 22′ N, 80° 32′ W; elevation 1,160 m at MLBS). MLBS is located on Salt Pond Mountain in the Appalachian Mountains of southwestern Virginia. The forest canopy included red oaks (*Quercus coccinea*, *Q. rubra*, and *Q. velutina*), white oaks (*Q. alba* and *Q. montana*), maples (*Acer rubrum* and *A. saccharum*), hickories (*Carya glabra*, *C. ovata*, and *C. tomentosa*), birches (*Betula alleghaniensis* and *B. lenta*), American beech (*Fagus grandifolia*), and yellow poplar (*Liriodendron tulipifera*). Scattered conifers intermingled with deciduous trees included pines (*Pinus strobus* and *P. rigida*), hemlocks (*Tsuga canadensis* and *T. caroliniana*), and red spruce (*Picea rubens*). Representative shrubs included striped maple (*A. pensylvanicum*), witch-hazel (*Hamamelis virginiana*), rhododendron (*Rhododendron maximum*), mountain-laurel (*Kalmia latifolia*), red maple, serviceberry (*Amelanchier arborea*), and American chestnut (*Castanea dentata*).

Recording songs.—We recorded songs of Red-eyed and Blue-headed vireos on Butt Mountain (located approximately 9 km southwest of MLBS) to ensure that playback experiments were conducted using songs representing the local dialect of each species (Kroodsma 1986, 1989). We recorded Blue-headed Vireo songs (*n* = 5) from 2 to 4 May 1997 and Red-eyed Vireo songs (*n* = 5) from 30 May to 1 June 1997. Recordings were made on Sony High Fidelity (Type I, normal bias) cassette tapes using a Marantz PMD-430 tape recorder and a Sennheiser ME66 shotgun microphone equipped with a K6C power supply, MZS-6 shock mount, and a MZW-66 windscreen (Saul Mineroff Electronics,

New York). We transferred recordings containing at least 60 consecutive seconds of song (i.e., recordings were not spliced together) to TDK 1M 1-min loop cassettes using a Sony CFD-545 dual cassette dubbing system. One-min loop tapes of five different individuals of each species were made for use in playback experiments.

Playback experiments.—We conducted playbacks at 200-m intervals along 20 parallel 1-km transects along Virginia St. Rt. 613 beginning 0.5 km north of MLBS. Transects were separated by 200 m. Because our emphasis in this study was to determine how interspecific interactions might affect habitat use, we chose to conduct playbacks along transects (as opposed to within known territories). This approach allowed us to estimate the frequency with which interspecific aggression is likely to impinge on site selection over the habitat as a whole. During 1997, we conducted playback experiments from 12 June to 13 July, a period coinciding with late incubation through nestling and fledgling stages of the breeding season (James 1998, Cimprich et al. 2000). During 1998, we conducted playbacks from 8 May to 2 June, a period coinciding with territory establishment, nest initiation, and early incubation (James 1998, Cimprich et al. 2000). All experiments were conducted between 05:00 and 10:30 (EST) to minimize time-of-day effects. Different transects were established each year so that no site was used more than once for playbacks.

We conducted each 6-min playback trial in two 3-min periods (Rice 1978a). During the pretrial period (first 3 min), we noted all Red-eyed and Blue-headed vireos heard (song or call) or seen in order to estimate the relative abundance of each species. During the trial period (second 3 min), we broadcast a randomly selected song tape using a Radio Shack CTR-96 hand-held tape recorder (volume setting 7) equipped with a Realistic 10A2 speaker set at maximum volume. Individuals were considered to be responding to playback if they approached the playback area (≤10 m of the speaker) and appeared to search for the source of the song. Although responses to song playback may be graded (e.g., increased song rate with no approach to the playback speaker), and we did detect graded responses to conspecific playback in both species, we did not detect graded responses to heterospecific playback in either species (SPH and CRC unpubl. data). Thus, we chose the above discrete measure of response for our analyses. We conducted 61 playback trials (28 of Blue-headed Vireos and 33 of Red-eyed Vireos) during 1997 and 59 playback trials (28 of Blue-headed Vireos and 31 of Red-eyed Vireos) during 1998.

Territory mapping.—We mapped Red-eyed and Blue-headed vireo territories in a 36-ha area (gridded at 50-m intervals) centered around MLBS (about 0.5 km south of the playback areas) following the recommendations of Bibby et al. (1993). Once or twice weekly, we walked a route passing ≤50 m of each point within the territory mapping area and recorded each Red-eyed or Blue-headed vireo located visually or audibly on a census map to the nearest 10 m. An

unmarked map was used during each visit to reduce bias from previous registrations. Data were compiled on a composite territory map at the end of each field season and territories were determined following the recommendations of Bibby et al. (1993:50–53).

Habitat characteristics.—We selected plots to quantify habitat characteristics within territories of Red-eyed ($n = 43$) and Blue-headed ($n = 32$) vireos throughout the study site (mapping and playback areas). One plot per territory was centered on a tree where Red-eyed or Blue-headed vireos were observed singing and foraging. An 11.3-m radius plot was established around each plot center and habitat characteristics were quantified (James and Shugart 1970, James 1971). All trees (woody stems ≥10 cm dbh) were identified and dbh was recorded. Shrubs (woody stems ≥1.4 m tall and <10 cm dbh) were quantified along four 11.3- × 1.5-m transects along the cardinal directions of a compass, and canopy cover was estimated at 13 points (one center point and four points along each transect; points were approximately 2.5 m apart) within each plot.

Data analysis.—We examined playback response data using analysis of frequencies (*G*-test) to determine if Red-eyed and Blue-headed vireos differed in their likelihood to respond to playback of conspecific and heterospecific song during each year. We assessed whether Red-eyed and Blue-headed vireo habitats differed in (1) overall structure as described by number of trees and shrubs, basal area, and canopy cover; (2) tree species composition; or (3) shrub species composition. Our approach was to carry out univariate comparisons of the individual variables followed by MANOVA of all the variables describing a particular habitat feature (structure, tree composition, shrub composition). Univariate comparisons of Red-eyed and Blue-headed vireo habitat features were made using *t*-tests (when the parametric assumptions of normality and homoscedasticity were met) and a Wilcoxon two-sample test (when the parametric assumption of normality was not met). In cases where MANOVA indicated a significant difference between species, we used a canonical discriminant analysis to identify the variables that best discriminated Red-eyed and Blue-headed vireo habitat.

We pooled the habitat data from both years. We included in the tree species analysis only those species or species groups that occurred at a frequency of ≥13 individuals in the total sample: REDOAK (red oaks, comprising *Quercus coccinea*, *Q. rubra*, and *Q. velutina*; 32% of trees sampled), REDMAP (red maple; 21%), WHTOAK (white oaks, comprising *Q. montana* and *Q. alba*; 12%), SNAG (standing dead trees; 12%), CONFER (conifers, comprising *T. canadensis*, *Pinus strobus*, and *P. rigida*; 5%), BLKGUM (black gum, *Nyssa sylvatica*; 5%), SRVBER (service berry; 3%), BLKBIR (black birch, *Betula lenta*; 3%), HICKY (hickories, comprising *Carya cordiformis*, *C. glabra*, *C. ovata*, and *C. tomentosa*; 2%), BLKCHY (black cherry, *Prunus serotina*; 1%), YELBIR (yellow birch, *B. alleghaniensis*; 1%), CUCTRE (cucumber magno-

lia, *Magnolia acuminata*; 1%), STRMAP (striped maple; 0.7%), ABEECH (American beech; 0.6%), and BLKLOC (black locust; 0.6%).

We included in the shrub species analysis only those species or species groups that occurred at a frequency of ≥11 individuals in the data set: STRMAP (37%), WITHAZ (witch-hazel; 17%), AMCNUT (American chestnut; 7%), SRVBER (6%), KALMIA (mountain-laurel; 6%), SNAG (6%), REDMAP (4%), CONFER (3%), RHODOD (rhododendron; 3%), VACCIN (*Vaccinium* spp.; 3%), and BLKGUM (2%).

We used Dunn-Sidák correction for multiple inferences (Sokal and Rohlf 1995:241) to hold experimentwise error at α = 0.05 for each family of *a priori* tests. A family of tests is defined as all comparisons falling under the same general null hypothesis (Chandler 1995). For example, the overall comparison of Red-eyed and Blue-headed vireo responses to conspecific song comprised four tests of the null hypothesis that Red-eyed and Blue-headed vireos respond similarly to their own species song. Similarly, heterospecific playback experiments comprised five tests and habitat characteristics comprised seven tests. *P* values of standard analyses were ordered from smallest to largest to determine significance by the Dunn-Sidák correction. The comparison with the smallest *P* value was considered significant when $P \leq 1 - (1 - \alpha)^{1/k}$, where α is the experimentwise error rate and *k* is the number of tests (Sokal and Rohlf 1995:241). The second smallest *P* value was considered significant when $P \leq 1 - (1 - \alpha)^{1/k-1}$, and so on. Uncorrected *P* values are reported in the text and significant results after Dunn-Sidák correction are indicated with asterisks.

RESULTS

Relative abundance.—During the 1997 and 1998 field seasons combined, we detected 150 Red-eyed Vireos (74 and 76, respectively) and 74 Blue-headed Vireos (38 and 36, respectively) during the preplayback period. Thus, Red-eyed Vireos outnumbered Blue-headed Vireos approximately 2:1 on our study area.

Response to conspecific song.—Red-eyed Vireos responded to playback of conspecific song 45% (15/33) of the time, whereas Blue-headed Vireos responded 29% (8/28) of the time during 1997. During 1998, Red-eyed Vireos responded 61% (19/31) of the time and Blue-headed Vireos responded 29% (8/28) of the time. Red-eyed and Blue-headed vireos did not differ significantly between years in their likelihood to respond to conspecific song (Red-eyed Vireo: $G = 1.62$, df = 1, $P = 0.20$; Blue-headed Vireo: $G = 0.00$, df = 1, $P = 1.00$). The relative response of the two species to playback of their own song did not differ significantly from their relative abundance on
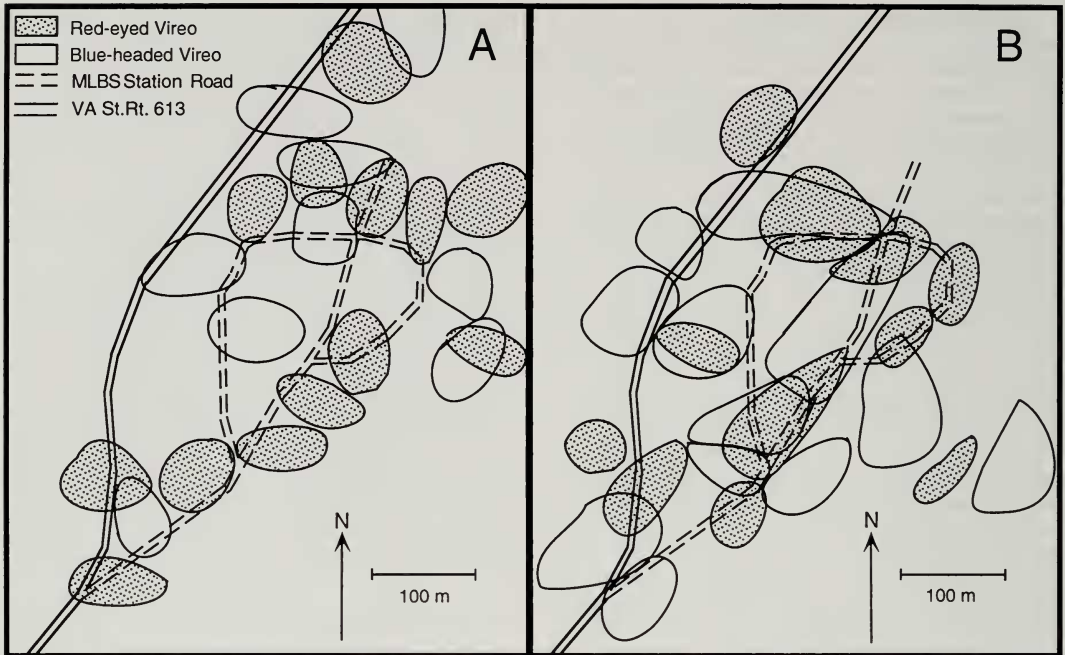
FIG. 1.   Territorial overlap by Red-eyed (*Vireo olivaceus*) and Blue-headed (*V. solitarius*) vireos at Mountain Lake Biological Station, southwestern Virginia, during (A) 1997 and (B) 1998. Territories were determined using the recommendations of Bibby et al. 1993.

the study site as indicated by preplayback counts (1997: $G = 0.006$, df $= 1$, $P = 0.94$; 1998: $G = 0.06$, df $= 1$, $P = 0.80$).

Response to heterospecific song.—Red-eyed Vireos responded to heterospecific song 11% (3/28) of the time whereas Blue-headed Vireos responded 0% (0/33) of the time during 1997. During 1998, Red-eyed Vireos responded 7% (2/28) and Blue-headed Vireos responded 3% (1/31) of the time. The response of each species to heterospecific song was consistent with their relative abundance in the habitat (1997: $G = 2.4$, df $= 1$, $P = 0.12$; 1998: $G = 1.5$, df $= 1$, $P = 0.21$).

Territory overlap.—Territories of Red-eyed and Blue-headed vireos overlapped at MLBS

during 1997 and 1998. During 1997, 5 of 13 (38%) Red-eyed Vireo territories overlapped Blue-headed Vireo territories, and 5 of 9 (56%) Blue-headed Vireo territories overlapped Red-eyed Vireo territories (Fig. 1A). Territorial overlap increased during 1998; 7 of 12 (58%) Red-eyed Vireo territories overlapped with Blue-headed Vireo territories, and 7 of 11 (64%) Blue-headed Vireo territories overlapped Red-eyed Vireo territories (Fig. 1B).

Habitat characteristics.—Although Blue-headed Vireos selected territories with a higher density of trees, Red-eyed and Blue-headed vireos occupied structurally similar habitats, whether structural variables were considered

TABLE 1.   Structure characteristics of Red-eyed (*Vireo olivaceus*) and Blue-headed (*V. solitarius*) vireo habitats at Mountain Lake Biological Station, southwestern Virginia, 1997–1998. Values are means ± SE. Only the number of trees per plot differed significantly.

Species (plots)	Basal area (cm^2)	Trees per plot*	Shrubs per plot	Percent canopy cover
Red-eyed Vireo (43)	12,427 ± 471	24 ± 1	14 ± 2	72 ± 2
Blue-headed Vireo (32)	12,884 ± 621	28 ± 2	16 ± 1	71 ± 2

* $t = 2.19$, df $= 73$, $P = 0.032$.
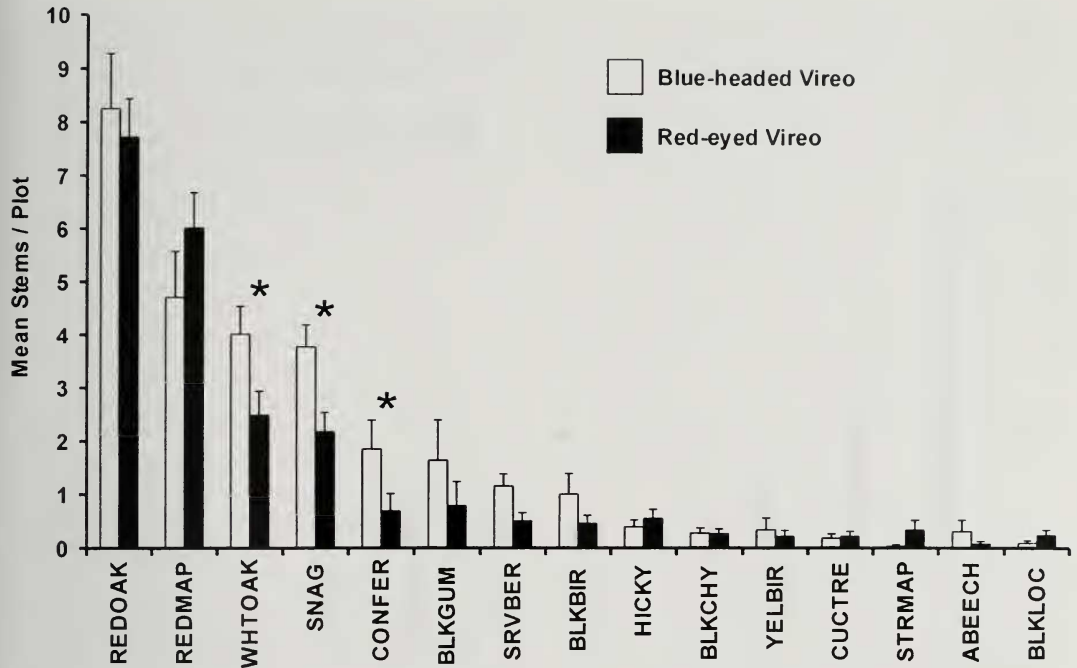
FIG. 2. Mean number of tree stems in Red-eyed (*Vireo olivaceus*, *n* = 43) and Blue-headed (*V. solitarius*, *n* = 32) vireo habitat plots at Mountain Lake Biological Station, southwestern Virginia, 1997–1998. Line above bar is 1 SE. Asterisks indicate significant differences between Red-eyed and Blue-headed vireo plots (WHTOAK and SNAG: *t*-test, adjusted *P* < 0.05; CONFER: Wilcoxon two-sample test, adjusted *P* < 0.05). Abbreviations for tree species classes and adjustment for *P* values are described in the text.

singularly (Table 1) or in a multivariate analysis of variance (MANOVA, Wilks' Lambda = 0.94, *P* = 0.43). Although structurally similar, univariate analysis characterized Blue-headed Vireo habitat as having significantly greater numbers of white oaks, conifers, and snags (Fig. 2). MANOVA indicated significant overall differences in tree species composition between vireo habitats (Wilks' Lambda = 0.703, *P* = 0.047) and canonical discriminant analysis showed that Red-eyed and Blue-headed vireo habitat is best discriminated based on the presence of striped maple and black locust (more common in Red-eyed Vireo habitat) and conifers and black birch (more common in Blue-headed Vireo habitat; Fig. 2). Red-eyed and Blue-headed vireo habitats did not differ significantly in shrub species composition, as indicated by univariate (Fig. 3) and multivariate analyses (MANOVA, Wilks' Lambda = 0.81, *P* = 0.68).

DISCUSSION

There is growing evidence that interspecific behavioral interactions within assemblages of vireos are geographically variable. For example, Red-eyed Vireos respond to sympatric congeners with (Rice 1978a, 1978b, 1978c) or without (James 1976, Robinson 1981) interspecific territoriality, depending on the species and location. Even in the absence of interspecific territoriality, Red-eyed Vireos may (Barlow et al. 1970, Robinson 1981) or may not (James 1976) show interspecific aggression. Our results from the southern Appalachians are consistent with the latter situation. Red-eyed and Blue-headed vireos lacked interspecific territoriality at Mountain Lake and showed low levels of interspecific aggression, as measured by response to heterospecific song. Greater response to song playbacks by Red-eyed Vireos was consistent with their greater relative abundance at Mountain Lake.

Given the lack of interspecific territoriality and aggression, previous studies of vireo assemblages suggest that Red-eyed and Blue-headed vireos at Mountain Lake should exhibit some other pattern of spatial segregation (James 1976). Red-eyed Vireos generally in-
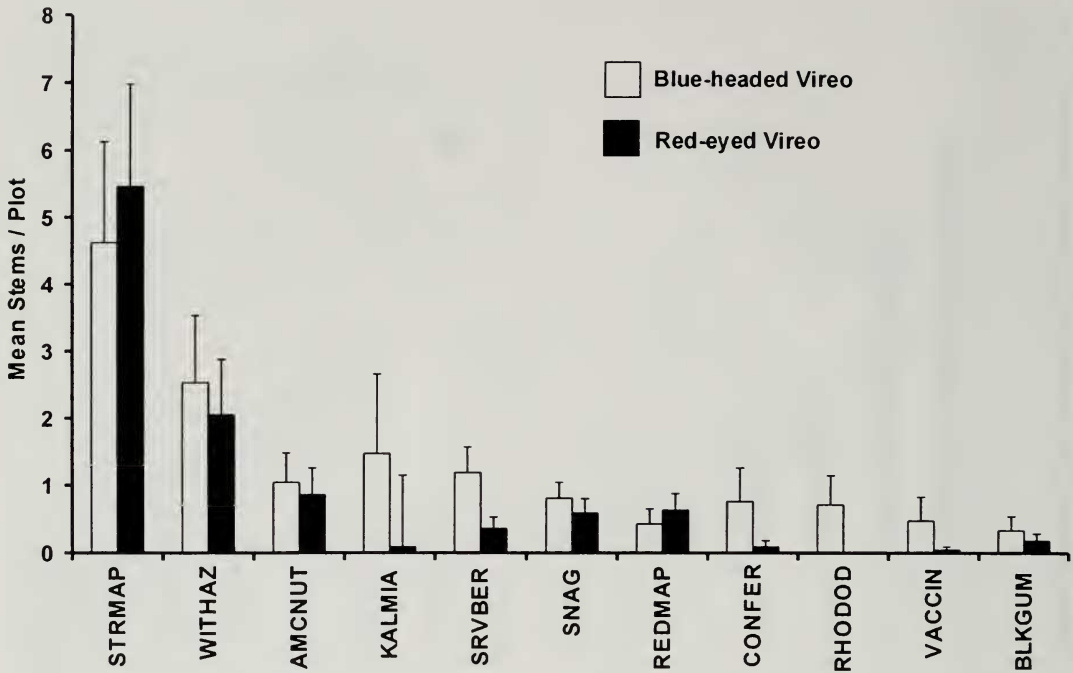
FIG. 3.   Mean number of shrub stems in Red-eyed (*Vireo olivaceus*, $n = 43$) and Blue-headed (*V. solitarius*, $n = 32$) vireo habitat plots at Mountain Lake Biological Station, southwestern Virginia, 1997–1998. Line above bar is 1 SE. There were no significant differences between Red-eyed and Blue-headed vireo plots. Abbreviations for shrub species classes are defined in the text.

habit mature deciduous forests (Bent 1950, Hamilton 1962, James 1971) with some shrubs in the understory (James 1971), whereas Blue-headed Vireos generally inhabit coniferous or mixed deciduous-coniferous forests with sparse understory shrubs (Bent 1950, Hamilton 1962, James 1998). These generalizations lead to an expectation that Red-eyed and Blue-headed vireos at Mountain Lake might occupy slightly different microhabitats within their overlapping territories.

This was not the case regarding habitat structure. Based on the locations of singing or foraging individuals, Red-eyed and Blue-headed vireos occupied sites with similar tree size, density, and canopy cover. Nevertheless, there were slight but detectable differences in the tree species composition of the sites where we observed the two species. We observed Blue-headed Vireos in areas with significantly more white oaks, conifers, and snags, whereas we found Red-eyed Vireos in habitats with a relatively high abundance of red oaks and red maple (Fig. 2). Interestingly, species segregation (based on canonical discriminant analysis) was strongest for tree species that formed a relatively minor component of the forest at Mountain Lake. The tendency of Blue-headed Vireos to occupy sites with more conifers at Mountain Lake is consistent with qualitative reports of Blue-headed Vireo habitat preference (Bent 1950, Hamilton 1962, James 1998).

The habitat differences we observed in vireos at Mountain Lake were subtle, as were those documented by Sherry (1979) and Sherry and Holmes (1988) for American Redstarts (*Setophaga ruticilla*) and Least Flycatchers (*Empidonax minimus*) in New Hampshire. However, interspecific aggression appears to play a smaller role in reinforcing habitat segregation in Red-eyed and Blue-headed vireos than it did for redstarts and flycatchers (Sherry 1979, Sherry and Holmes 1988).

Although spatial (horizontal) segregation at the scale of the territory was not apparent and minimal in terms of microhabitat use, it remains possible that Red-eyed and Blue-headed vireos coexist by segregating vertically within the habitat by using different foraging

zones or nest sites. However, we detected only minimal differences in foraging height (SPH and CRC unpubl. data) at Mountain Lake. Furthermore, Red-eyed and Blue-headed vireos apparently built nests at similar heights at our study site (SPH and CRC unpubl. data). Published observations from other areas of sympatry also have failed to reveal pronounced vertical segregation (Cimprich et al. 2000, James 1998).

Based on the results of this and other studies (Bent 1950; Hamilton 1962; James 1971, 1998), preliminary foraging data, and behavioral characteristics such as nest site selection, apparent ecological segregation between Red-eyed and Blue-headed vireos was minimal at our study site and atypical of most sympatric vireo pairs (Hamilton 1962, Cody 1985). Red-eyed and Blue-headed vireos showed greater similarity in habitat use in the southern Appalachians than in the northern part of their ranges, but they did not increase interspecific aggression or diverge in foraging strategy (Petit et al. 1990; SPH and CRC unpubl. data). We believe the similarity in habitat use at our study site is a result of the relative availability of these species' preferred habitats. In other words, we suggest that Red-eyed and Blue-headed vireos respond to their own individualistic habitat cues (James 1971, Collins et al. 1982, Martin and Thibault 1996), but the nature of the habitat at Mountain Lake (conifers and birches broadly interspersed among dominant oaks and maples) precludes clear segregation by habitat. Additionally, ecological mechanisms other than territoriality and microhabitat segregation may be important in structuring the coexistence between these two species in the southern Appalachians.

Northern and southern subspecies of Blue-headed Vireo (*Vireo s. solitarius* and *V. s. alticola*, respectively) show slight morphological differentiation (generally larger in the south; James 1998), which may explain the qualitatively different foraging strategies employed by this species in the northern and southern Appalachians (Rabenold 1978, Robinson and Holmes 1982, Petit et al. 1990). Comparing the foraging strategies of Red-eyed and Blue-headed vireos in the southern Appalachians may further clarify the ecological factors potentially influencing their coexistence. Furthermore, a comparative analysis of habitat availability, habitat use, and foraging ecology between northern and southern populations of Red-eyed Vireos and both subspecies of Blue-headed Vireo may be necessary to tease apart subtle ecological differences between these two species.

We conclude that interspecific aggression and habitat association play only a small role in the ecological segregation of Red-eyed and Blue-headed vireos in the southern Appalachians. Furthermore, we suggest that quantitative analysis of basic patterns of ecological segregation can still yield important insights concerning local community structure and may be important in directing future forest management decisions.

ACKNOWLEDGMENTS

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